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Morphological and Cytological Data on Southeastern United States Species of the Asplenium heterochroum–resiliens Complex

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In a recent issue of this JOURNAL, Wagner (1966) named a new species, *Asplenium heteroresiliens*. This paper supplies morphological and cytological data which support the hypothesis that Wagner's species is the $5x$ hybrid between a $4x$ sexual plant of *A. heterochroum* and an apogamous $3x$ plant of *A. resiliens*.

I am grateful to Mr. Thomas Darling, Jr., of Washington, D. C., who collected plants at Cat Hammock, near Sumterville, Sumter County, Florida, and Dr. E. S. Ford, who sent plants from near Gainesville, Alachua County, and from Columbia County, Florida, about 5 miles northwest of High Springs. These plants were received at the Botanical Gardens of the University of Michigan and grown in the greenhouse under optimum conditions until suitable meiotic stages developed. Chromosome numbers were determined; other observations are summarized in Table 1.

The Alachua County plant, identified as *A. heterochroum*, was a sexual hexaploid, $2n=216$, having 64 haploid spores per sporangium (*Pl. 19D; Pl. 20B, J*). The Sumter County plant, also identified as *A. heterochroum*, was found to be a sexual tetraploid, $2n=144$ (*Pl. 19C; Pl. 20C*). The third plant, from Co-

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TABLE 1. COMPARISON OF FOUR SPLEENWORTS (FROM LIVING PLANTS GROWN UNDER UNIFORM GREENHOUSE CONDITIONS, U.M. BOTANICAL GARDENS)

Taxon	*4x A. heterochroum*	*6x A. heterochroum*	*3x A. resiliens*	*5x A. heteroresiliens*
Source	Sumter Co., Fla.	Alachua Co., Fla.	Cheatham Co., Tenn.	Columbia Co., Fla.
Habit	Leaves mostly strict *(Pl. 19C)*	Leaves mostly strict *(Pl. 19D)*	Older, smaller leaves more spreading *(Pl. 19A)*	Older, smaller leaves somewhat spreading *(Pl. 19B)*
Leaf texture	Herbaceous	Herbaceous	Coriaceous	Subcoriaceous
Leaf and leaflet length	Small: lvs. to 12.5 cm; median pinnae to 8 mm	Larger: lvs. to 18.5 cm; pinnae to 8 mm.	Large: lvs. to 20 cm; pinnae to 13 mm	Moderate: lvs. to 16 cm; pinnae to 9 mm
Laminar color ("L," Villalobos, 1947)	Yellow-green, more lustrous (lightness 8-9; chromaticity 11°-12°)	Yellow-green, more lustrous (lightness 7-9; chromaticity 11°-12°)	Gray-green, dull (lightness 6-7; chromaticity 7°-8°)	Green, more dull; (lightness 5-8; chromaticity 7°-11°)
Pinna tips	Truncate-dentate *(Fig. 1C)*	Truncate-dentate *(Fig. 1D)*	Rounded, nearly smooth *(Fig. 1A)*	Rounded, smooth to crenate *(Fig. 1B)*
Angle of pinna attachments (upper ⅓ of leaf)	Right angles	Right angles	Oblique	Right angles

Anterior pinna margins			
Coarsely dentate	Coarsely dentate	Smooth, (mainly) undulate, or crenate	Dentate to (mainly) crenate
Anterior pinna auricles (lower 1/3 of leaf)			
Weakly developed, rounded-dentate	Weakly developed, rounded-dentate	Strongly developed, pointed, entire	Somewhat developed and pointed
Petiolules (upper 1/3 of leaf)			
Hardly visible to naked eye; pinnae nearly sessile	Hardly visible to naked eye; pinnae nearly sessile	Short, definite, c. 1/3-1/2 mm long, visible to naked eye	Pinnae nearly sessile
Sorus position (especially distal basicopic sori)			
Medial to inframedial *(Fig. 1C)*	Medial to inframedial *(Fig. 1D)*	Supramedial *(Fig. 1A)*	Medial *(Fig. 1B)*
Average number of forked veins (above the basal auricle)			
0.3 (0-1)	0.3 (0-1)	3.6 (2-5)	1.6 (0-4)
Rhizome scales			
Short; broad base narrowing gradually to apex *(Pl. 21G)*	Long; broad base narrowing gradually to apex *(Pl. 21F)*	Long; narrow entire length, becoming filiform *(Pl. 21H)*	Long; med.-wide base, narrowing to attenuate apex *(Pl. 21I)*
Epidermal cell sizes (Upper; Lower)			
Medium *(Pl. 21J)* c. 83.9μ; c. 109.7μ	Large *(Pl. 21K)* c. 98.9μ; c. 145.7μ	Small *(Pl. 21L)* c. 67.0μ; c. 96.3μ	Med. to lge. *(Pl. 21M)* c. 89.6μ; c. 141.6μ
Stomate length			
Short, c. 44.6μ	Long, c. 51.2μ	Very long, c. 56.2μ	Very long, c. 56.9μ
Spore length; degree of abortion			
(Pl. 20E) $2x$ spore, c. 35μ; minimal	*(Pl. 20F, J)* $3x$ spore, c. 41μ; minimal	*(Pl. 20G)* $3x$ spore, c. 42μ; considerable	*(Pl. 20H, I)* $5x$ spore, c. 47μ; considerable
Sporophytic chromosome number			
$2n=144$ *(Pl. 20C)*	$2n=216$ *(Pl. 20B)*	"$2n$"$=108$ *(Pl. 20A)*	"$2n$"$=180$ *(Pl. 20D)*

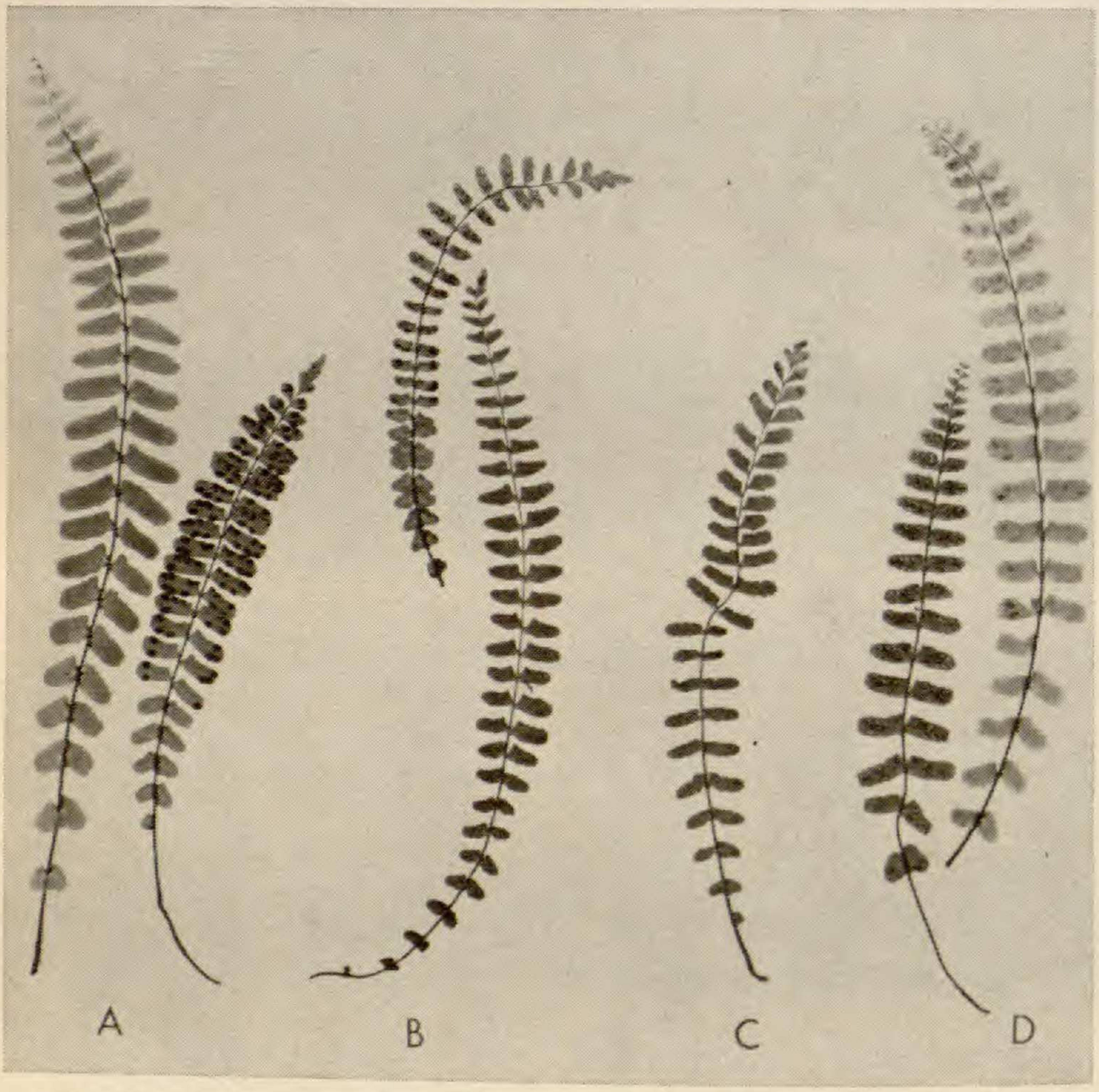


PLATE 19. FRONDS OF: A. A. RESILIENS. (CHEATHAM CO., TENN., *Wagner 9334*). B. A. HETERORESILIENS (COLUMBIA CO., FLA.). C. 4*x* A. HETEROCHROUM (SUMTER CO., FLA.). D. 6*x* A. HETEROCHROUM (ALACHUA CO., FLA.).

lumbia County, was neither a sexual $4x$ nor $6x$ plant, but rather an apogamous pentaploid. Its spore mother cells, containing 180 bivalents at meiosis, formed 32 diploid spores per sporangium (*Pl. 19B; Pl. 20D, I*).

It was first hypothesized that the apogamous $5x$ *A. heteroresiliens* was the hybrid between sexual $4x$ and $6x$ *A. heterochroum*. However, the latter two plants looked very much alike

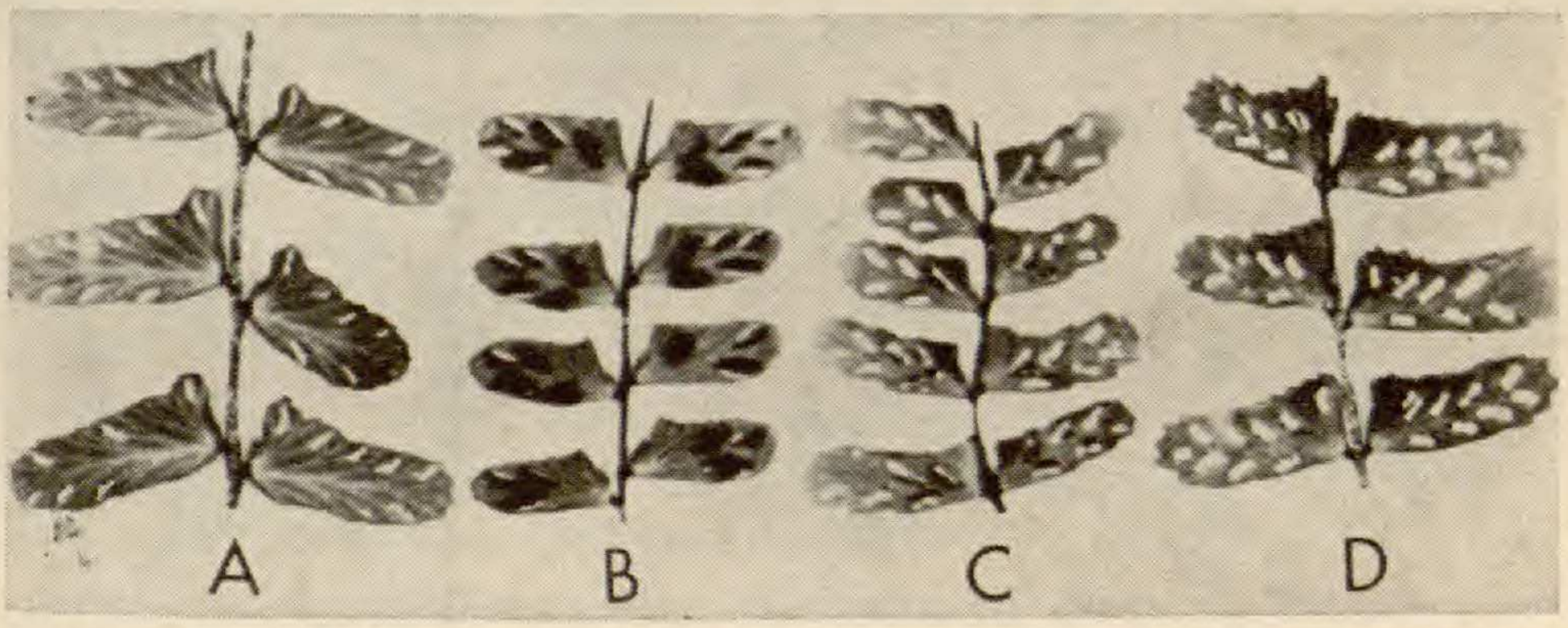
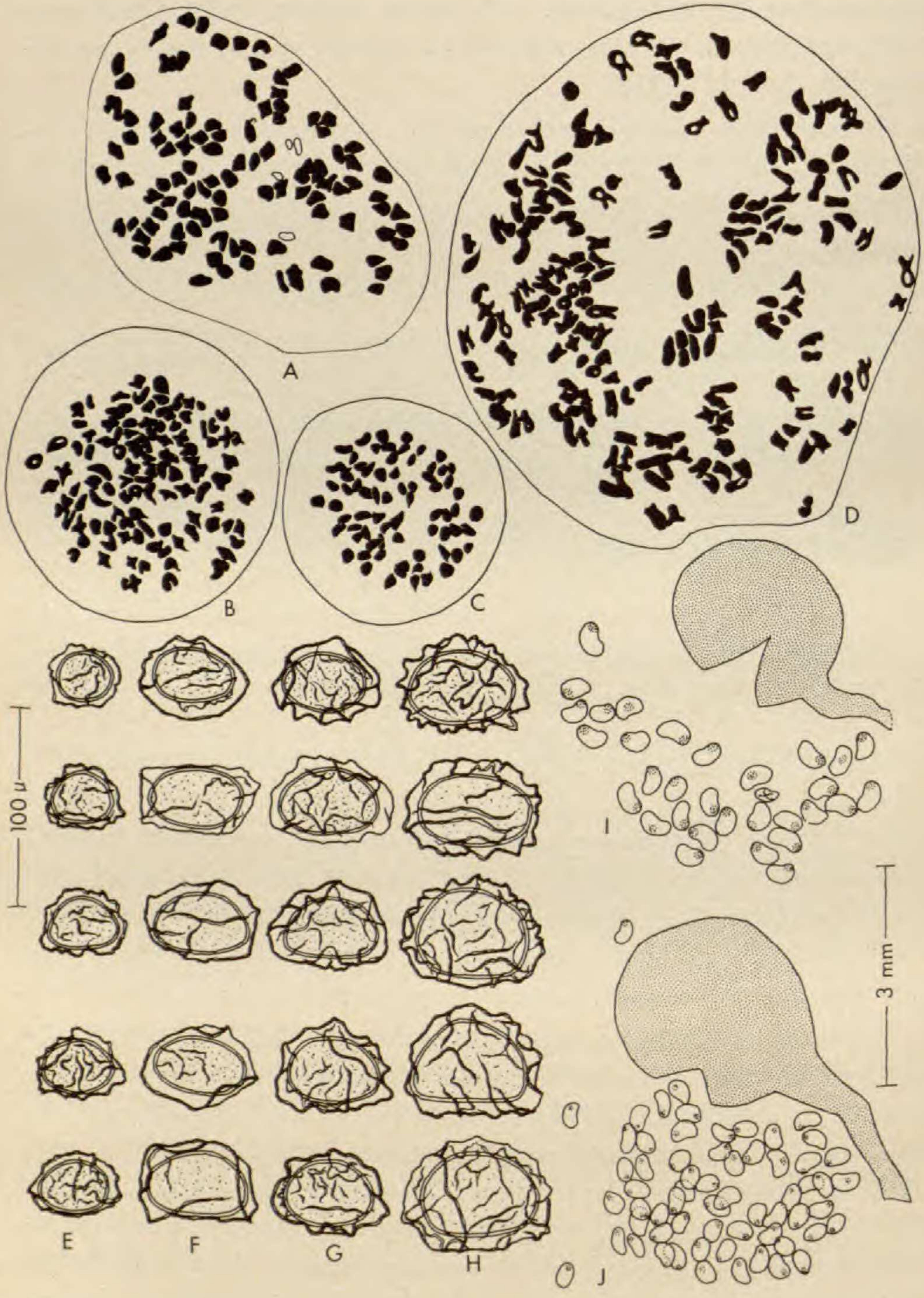


FIGURE 1. MEDIAN PINNAE OF: A. A. RESILIENS. B. A. HETERORESILIENS. C. $4x$ A. HETEROCHROUM. D. $6x$ A. HETEROCHROUM.

morphologically except in size (*Pl. 19C* and *Fig. 1C* versus *Pl. 19D* and *Fig. 1D*), whereas the former seemed to differ on gross examination, particularly in its darker color. A study of anatomical and morphological characters was then undertaken, including those of *A. resiliens*, an apogamous triploid with both "n" and "$2n$"=108 (*Pl. 19A*), which closely resembles *A. heterochroum* and *A. heteroresiliens*.

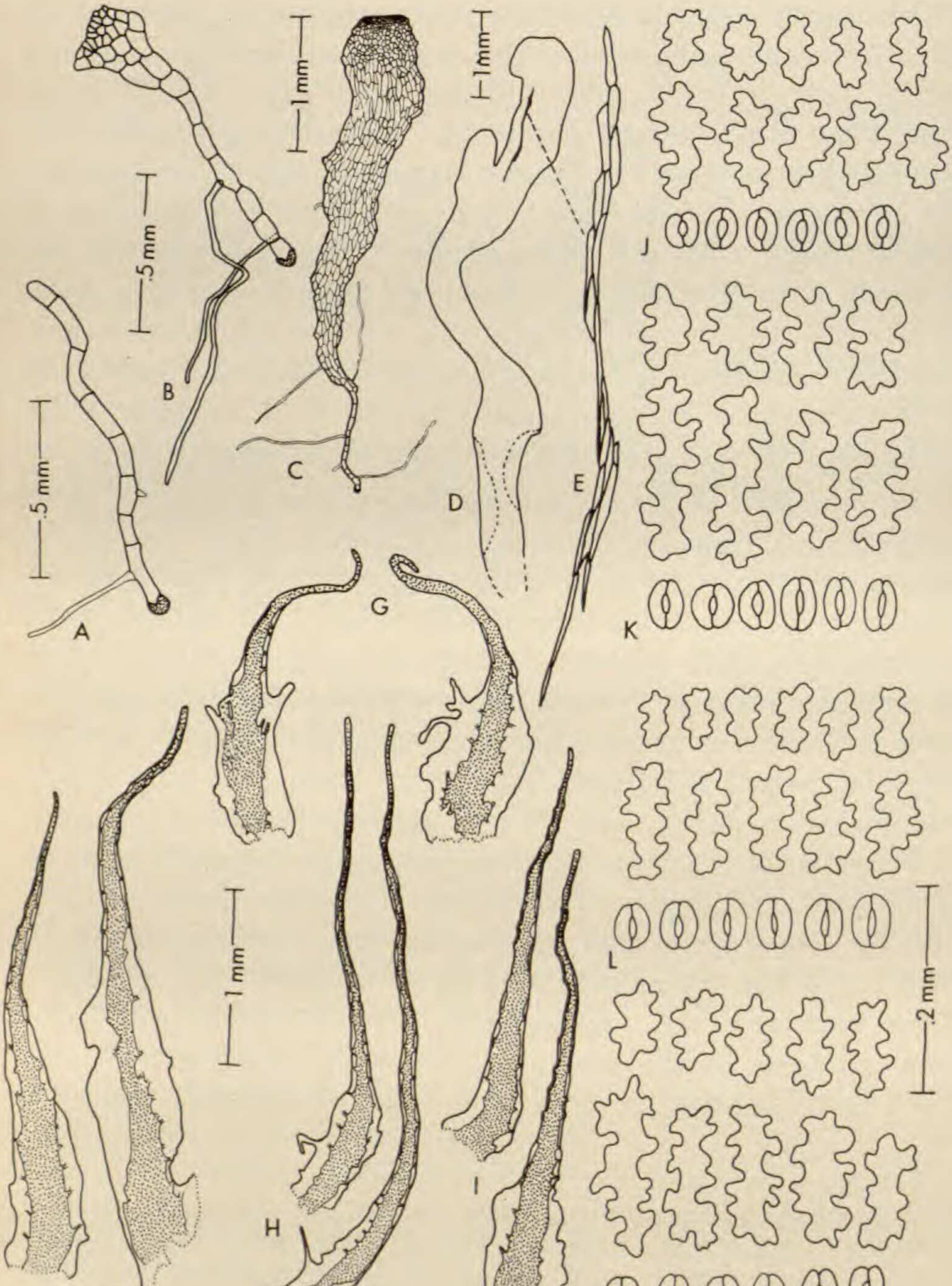
The results of the investigation led to the conclusion that the $5x$ hybrid originated as the cross between $4x$ *A. heterochroum* and $3x$ *A. resiliens*. As shown in *Table 1, Plates 19* and *20F–I*, and *Fig. 1*, the $5x$ hybrid is intermediate between the above parents in growth habit, leaf texture, leaf and leaflet length, lamina color, pinna tips, anterior pinna margins, anterior pinna auricles (lower 1/3 of leaf), sorus position, degree of forking in the sorus-bearing veins above the basal auricles, and rhizome scales.


A
B
C
D
100 µ
E
F
G
H
I
J
3 mm

One of the characters of 3*x* *A. resiliens* is its large stomates, which nearly equal those of 6*x* *A. heterochroum.* Those of 4*x* *A. heterochroum* are small. The stomates of the pentaploid are larger than any of the above plants, being even slightly larger than those of the sexual hexaploid. Spore characteristics (*Pl. 20E–H*) also indicate the hybrid nature of 5*x* *A. heteroresiliens*: the spores are intermediate in size and relative convolution of the perispore. The 2*x* spores of 4*x* *A. heterochroum* are the smallest, averaging 35μ in length, and have a relatively large number of convolutions. Triploid *A. resiliens* spores are larger, averaging 42μ, and are also quite convoluted. Hexaploid *A. heterochroum* has 3*x* spores similar in size to *A. resiliens,* averaging 41μ, but with a much less convoluted perispore.

Not only does *A. heteroresiliens* share the morphological characteristics of its parents, but it has also evidently inherited the apogamous life cycle of *A. resiliens.* Although the 32-spored sporangia indicated this type of life cycle for the hybrid, spore cultures were made in order to study the complete life cycle and to confirm apogamy. Fronds were washed under violently running tap water to remove foreign spores, placed between clean sheets of paper, and dried (away from heat) in a plant press. The spores were then sown on agar plates containing 1½% agar in Beijerinck's nutrient solution. Within two weeks the spores germinated and began to form long uniseriate filaments (*Pl. 21A–C*). In three to four months they had greatly increased in length and also somewhat in width. Antheridia but no archegonia were observed. Sporophytes were budded off from the lower surfaces in the proximal half of the gametophytes; the distal half continued to grow, often being considerably narrower

PLATE 20. CHROMOSOMES OF: A. A. RESILIENS (*Wagner 9333*), 106^{II} $+4^{I}$. B. 6*x* A. HETEROCHROUM (UMBG 21690), 108^{II}. C. 4*x* A. HETEROCHROUM (UMBG, SUMTER CO., FLA.), 72^{II}. D. A. HETERORESILIENS (UMBG, 21689), 178^{II} (c. 180^{II}). E. 2*x* SPORES OF 4*x* A. HETEROCHROUM. F. 3*x* SPORES OF 6*x* A. HETEROCHROUM. G. 3*x* SPORES OF 3*x* A. RESILIENS. H. 5*x* SPORES OF 5*x* A. HETERORESILIENS. I. A. HETERORESILIENS, 32 SPORES PER SPORANGIUM. J. 6*x* A. HETEROCHROUM, 64 SPORES PER SPORANGIUM.


.5 mm
B
.5 mm
A
1 mm
C
1 mm
D
E
J
K
G
1 mm
F
H
I
L
.2 mm
M

than the middle portion. This long upper half was multiseriate and appeared, under 400× magnification, to have vascular tissue running through it. About seven months after the spores were sown, clearings were made of 30 gametophytes, most of which had developed tracheids (*Pl. 21D, E*). This was true whether or not the gametophytes had produced sporophytes. In my opinion, the regular occurrence of vascular tissue in fern gametophytes in positions separate from sporophytic buds is an unusual phenomenon.

Despite the clear relationships of the species discussed here, the situation involving other taxa in this complex—particularly those outside of Florida—is far more complicated and will involve much further study. For example, the existence of $4x$ and $6x$ *A. heterochroum* presupposes the past or present existence of $2x$ *A. heterochroum*. Spore measurements made on many herbarium specimens from the West Indies indicate that $2x$ plants of this species do exist. Also, the existence of a $6x$ form of *A. heteroresiliens* can be anticipated. Such an apogamous hybrid should be sought in areas where the potential parents, sexual $6x$ *A. heterochroum* and apogamous $3x$ *A. resiliens*, co-exist. The occurrence of several other genomic conditions in backcross hybrids can be hypothesized, and presumably they are occasionally produced in nature.

Voucher Specimens (all in MICH):

$4x$ *Asplenium heterochroum:* Cat Hammock, near Sumterville, Sumter County, Florida, Nov. 12, 1960, *Thomas Darling, Jr.* (UMBG).

$6x$ *Asplenium heterochroum:* Alachua County, Florida, Sept. 8, 1960, *E. S. Ford* (UMBG 21690).

$5x$ *Asplenium heteroresiliens:* Columbia County, Florida, Sept. 8, 1960, *E. S. Ford* (UMBG 21689).

PLATE 21. A, B. EARLY GAMETOPHYTE STAGES OF A. HETERORESILIENS. C. TWO-MONTH OLD GAMETOPHYTE OF A. HETERORESILIENS. D, E. GAMETOPHYTE SHOWING LOCATION OF AND ENLARGED DRAWING OF TRACHEARY TISSUE OF A. HETERORESILIENS. RHIZOME SCALES OF: F. $6x$ A. HETEROCHROUM. G. $4x$ A. HETEROCHROUM. H. A. RESILIENS. I. A. HETERORESILIENS. UPPER AND LOWER EPIDERMAL CELLS AND STOMATES OF: J. $4x$ A. HETEROCHROUM. K. $6x$ A. HETEROCHROUM. L. A. RESILIENS. M. A. HETERORESILIENS.

3*x Asplenium resiliens:* Big Marrowbone Creek, about ¼ mi. E of Tenn. Route 1W, Ashton City Road, Cheatham County, Tennessee, Oct. 23, 1960, *W. H. Wagner, Jr., 9333.*

Additional specimens of *Asplenium heteroresiliens* examined:

FLORIDA. **Columbia Co.**: between High Springs and Fort White, on open moist rocks in open woods, *D. S. Correll* 6449A (GH); about 3 mi. W of High Springs, limestone ledges, deciduous woods, *R. K. Godfrey 55355* and *H. Kurz* (GH). **Jackson Co.**: Marianna Caverns State Park, on limestone ledges in deciduous woods, *R. K. Godfrey 55333* (GH); near Florida Caverns State Park, on rocky ground, *J. B. McFarlin 11438a* (US); Natural Bridge, near Marianna, on rocks, Dec. 5–6, 1934, *J. K. Small & Wm. A. Knight* (NY); Florida Caverns State Park, locality 2, just S of main picnic grounds, among outcroppings of Marianna limestone, *W. H. Wagner 62044, R. K. Godfrey,* and *R. S. Mitchell* (MICH); **Liberty-Gadsden Co. Line**: shaded rocks, Appalachicola River, near Aspalaga, *A. H. Curtiss 3720* (GH, NY, US, Barnard College); E side of Appalachicola River at Aspalaga, with *A. platyneuron,* along tops of "weedy" boulders, *W. H. Wagner 62034, R. K. Godfrey* and *R. Mitchell* (MICH).

GEORGIA. "Collected on mortar between rocks of an old wall in the SE part of the state," *Donald Blake,* Sept. 8, 1963. (according to Duncan and Blake, 1965).

SOUTH CAROLINA. **Berkeley Co.** (erroneously listed as Charleston Co. by Wagner, in Radford et al., 1964): Enteric Springs, Santee Canal, *H. W. Ravenel, s. n.* (GH).

NORTH CAROLINA. **Bladen Co.**: 8 mi. SE of Elizabethtown, calcareous sandstone in beech woods, near Walker's Bluff, on Cape Fear River, *A. E. Radford 6854* (NCU). **Jones Co.**: 6.5 mi. E of Pollocksville, on consolidated marl rocks and ledges along Island Creek, *R. K. Godfrey 52238* and *E. E. Radford* (NCU); Marl outcrop in hardwood forest on Island Creek, *A. E. Radford 6782* and *G. R. Cooley; ibid., A. E. Radford 5722, 6059* (NCU); Limestone in woods on Reedy Creek, *A. E. Radford 5639* (NCU); 5 mi. S of New Bern, marl outcrop on Island Creek, Aug. 8, 1954, *Silliman & Munson* (NCU). **New Hanover Co.**: Wilmington, *M. A. Curtis* in 1831 (NCU).

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Some New Combinations in Thelypteris

C. V. MORTON

In 1959,[1] I showed that *Hemionitis pozoi* Lagasca[2] had long been misidentified as being a species of *Pleurosorus* but that actually it was the earliest name for the fern that had been called *Dryopteris africana* C. Chr. in the Index Filicum. This species belongs to *Thelypteris* subg. *Cyclosorus* sect. *Leptogramma* (J. Smith) Morton,[3] as I have classified this group. Some workers, e.g. Alston, have considered *Leptogramma* as a genus, but it seems to be no more than a section of subg. *Cyclosorus* with the sori elongate and exindusiate. Such elongate sori occur in other groups of *Thelypteris* (e.g. *Meniscium*) and in some species otherwise typical of the section *Lastrea*, e.g. *Dryopteris linkiana* and others, not yet transferred to *Thelypteris*.

The latest worker on this group, Dr. K. Iwatsuki, has treated *Leptogramma* as *Stegnogramma* Blume sect. *Leptogramma*,[4] but he has not adduced any convincing reasons for recognizing *Stegnogramma* as distinct from *Thelypteris*. In a more recent paper,[5] Iwatsuki has summarized the characters of *Stegnogramma* as follows: "Short rhizome with well marked collenchymatous tissues, the pinnate or pinnatifid fronds having the indistinct apical pinnae, the exindusiate sori elongate along the

[1] Sur la nomenclature de deux Fougères rares d'Espagne. Bull. Soc. Bot. France **106**: 231–234. 1959.
[2] Nov. Gen. et Sp. 33. 1816.
[3] Amer. Fern J. **53**: 153. 1963.
[4] Acta Phytotax. Geobot. **19**: 116. 1963.
[5] Mem. Coll. Sci. Univ. Kyoto, Ser. B, **31**: 19. 1964.